APHROPHYLLUM (RUGOSA) FROM LOWER CARBONIFEROUS LIMESTONES NEAR BINGARA, NEW SOUTH WALES

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(Communicated by Mr. R. H. Anderson)

(Plate xiii)

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Synopsis

The hystero-ontogeny of the type species of *Aphrophyllum*, *A. hallense* Smith, is described and *A. smithi*, sp. nov. is proposed. Both species are known only from Viséan (Lower Carboniferous) limestones at Halls Creek, near Bingara. Some similarities between the youthful and adult characters of *A. hallense* and those of *Thysanophyllum orientale* Nicholson and Thomson, type species of *Thysanophyllum*, and *Lonsdaleia* spp. suggest that *Aphrophyllum* may lie with the *Lonsdaleiidae*; other features, however, suggest that it lies in a separate, new family of rugose corals.

Introduction

Studies of Lower Carboniferous corals from New South Wales by Pickett (1967) and work in progress by the writer on Queensland forms have shown *Aphrophyllum* Smith to be an important and diverse genus endemic to the Viséan of eastern Australia. Its affinities are in doubt, with Smith (1920) and Jones (1933) suggesting a possible relationship with *Endophyllum* Edwards and Haime, Hill (1956) and Dobrolyubova (1962) relating it to *Palaeosmilia* Edwards and Haime, and Pickett (1967) placing the genus with the Lonsdaleiidae. With the intention of clarifying this problem, the following discussion is devoted to the details of the hystero-ontogeny of its type species *A. hallense* Smith. *Aphrophyllum smithi*, sp. nov., which is also described herein, provides some measure of the variability of the genus in the area of provenance of its type species.

Material for this study is from limestones at Halls Creek, some 17 miles south of Bingara, New South Wales (Text-fig. 1). Pickett (1967) considered these beds to be Middle Viséan in age and correlated them with the upper part of the Namoi Formation.

All fossil and locality numbers ("F" and "L" numbers) are registered in the catalogue of the Department of Geology and Mineralology, University of Queensland, Brisbane with the exception of those prefixed with "AM" which are in the Australian Museum, Sydney, and with "BM", in the British Museum (Natural History), London. The terminology applied to hystero-ontogeny is that as outlined by Jull (1965).

Systematic Description

Genus Aphrophyllum Smith

Aphrophyllum hallense Smith

(Pl. xiii, figs 1–3; Text-fig. 2)

Holotype: AM F17640 (not F17648 or F17684 as quoted respectively by Hill, 1934, p. 73 and Pickett, 1967, p. 29) with thin sections AM1036-38-39-40 in the Australian Museum, Sydney (listed as B8 by Smith, 1920, p. 64) and A5051 in the Sedgwick Museum, Cambridge.

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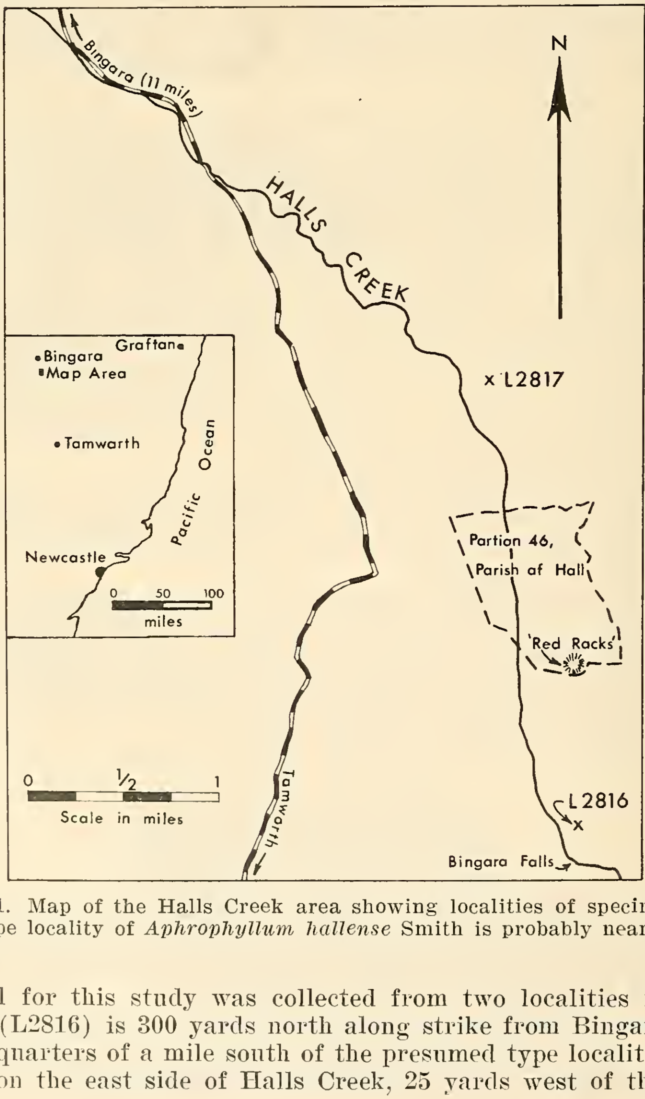
Locality and Age: The species is known only from a few localities at probably nearly the same stratigraphic horizon in Viséan limestones in the vicinity of Halls Creek, in Parish Hall, County Murchison, some 17 miles south of Bingara, New South Wales. Smith (1920, p. 51) in proposing the species, did not list a specific locality in these limestones for the holotoype and paratype. However, Benson who collected the material, reported (1917, p. 242) a fauna in this limestone in Portion 46, Parish Hall. As this is his only mention of a fossiliferous limestone in the area, presumably this is the type locality. I did not visit this spot during my trip to the area in 1964, but Mr. F. W. Mitchell, property owner on Halls Creek, who provided accurate information on other outcrops of the limestone, described to me the occurrence of a fairly prominent limestone outcrop immediately west of Red Rocks, a locality marked in Portion 46 of the Parish Map (see Text-fig. 1). This is possibly coincident with Professor Benson's collecting site.



Text.-fig. 1. Map of the Halls Creek area showing localities of specimens collected. Site of the type locality of *Aphrophyllum hallense* Smith is probably near "Red Rocks".

Material for this study was collected from two localities in this limestone. One (L2816) is 300 yards north along strike from Bingara Falls and about three-quarters of a mile south of the presumed type locality. The other (L2817) is on the east side of Halls Creek, 25 yards west of the serpentine and approximately one and one-half miles north of Benson's site. The limestones outcrop discontinuously in the area but the three localities are likely to prove to be nearly at the same horizon. There is no doubt that all material in question is conspecific.

Diagnosis: Cerioid, with irregularly shaped corallites averaging 18 mm. in diameter; usually 20 to 24 septa of each of two orders are present; the long often pinnately arranged major septa sometimes meet at the axis to form an irregular axial structure, and the minor septa are well developed; lonsdaleoid dissepiments occupy a variably wide zone and are naotically modified in part; tabulae are domed with flat or upturned ends; increase is lateral, rarely parricidal peripheral; trabeculae are monacanthne.

Description: A. Adult characters. Smith (1920), Hill (1934) and Pickett (1967) have all described the adult characters in adequate detail. Pickett (1967) placed in *Nothaphrophyllum gregarium* Pickett the specimen from Chatham Quarry, Taree, considered by Hill (1934) to belong to the present species.

B. Hystero-ontogeny. All known representatives of *A. hallense* are more or less crushed and this, together with the abundant stereome in the species which tends to obscure detail, and the fact that the axial septa are not obvious, makes the study of corallite development difficult. Amongst eleven coralla, only F46028 from L2816 yielded nearly complete details of hystero-ontogeny from examination of closely spaced acetate peel sections of the specimen. The following description is based principally on one corallite of this specimen, illustrated in Text-fig. 2. In general detail, this example of corallite development is typical of other youthful corallites which were observed in thin sections from other specimens including the holotype. Figure references, viz. F46028/18–23, refer to details in Text-fig. 2.

Lateral increase.

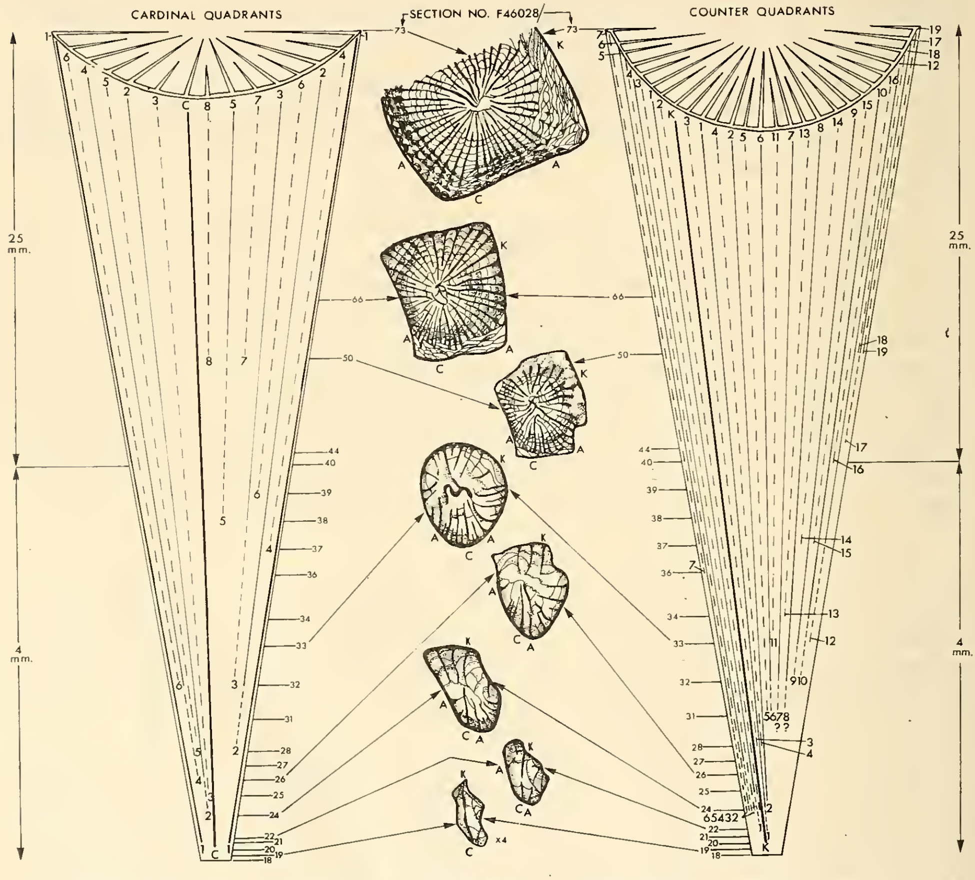
Increase is typically lateral but parricidal peripheral increase has been observed in one instance, this being described after the section on lateral increase. The laterally arising corallite developed within the lonsdaleoid dissepimentarium of the parent and all of its septa are independently inserted; they do not represent continuation of growth of parts of the septa of the parent. Stereome is abundant throughout development.

Hystero-brephic stage (F46028/18–23). The daughter corallite is first obvious as a small area within the lonsdaleoid dissepiments of the parent, and approximately 0·25 mm. distally axial septa appear. The axial plane is orientated radially to the axis of the parent with the cardinal septum on the outer side, furthest from the axis of the parent. Axial septa are initially united but almost immediately separate into counter and cardinal septa which never come into direct contact with each other again during development. Simultaneous with their separation is the appearance of alar septa, followed shortly by counter-lateral septa. After the shortening of the axial septa, none of the six septa are in contact during this stage of development which ranges over approximately 0·45 mm. of growth.

Hystero-neanic stage (F46028/24-38): This stage commences with the appearance of metasepta, and includes most of the septal insertion in the daughter corallite. Insertion is somewhat irregular, with septa arising from the wall of the corallite in fossulae which are not obvious. Newly inserted septa are not contratingent.

Most major septa are inserted before minor septa in a regular manner in the right cardinal quadrant. Insertion in the left cardinal quadrant would probably have been similar had not this side of the corallite been constricted during development with the result that major septum number 4 in this quadrant is late in appearing.

Insertion in the counter quadrants is characterized by periods of rapid insertion of major and minor septa. In general, major septa alternate with minor septa in order of appearance. A disproportionately large number of septa are inserted in the left counter quadrant (the reverse of the diagrammatic corallite in Text-fig. 2), resulting in the lateral migration of the counter



Text-fig. 2. Hystero-ontogeny in *Aphrophyllum hallense* Smith, F46028, from L2816. The diagrammatic representations of cardinal and counter quadrants illustrate the order of septal insertion; note the change in vertical scale. C= cardinal septum; K= counter septum; A= alar septum; solid lines= long major septa; short dashed lines= short major septa; long dashed lines= minor septa. Number 1 septa in the cardinal quadrants are alar septa. Numbers opposite the diagrammatic quadrants are those of pertinent acetate peel sections. Numbers 18 to 23 are through the hystero-brephic stage, 24-38 through the hystero-neanic stage, 39-72 through the late neanic stage, and 73 through the ephebic stage. Lower five corallites × 2·2, upper three corallites × 1·1.

septum during corallite growth so that axial septa cease to lie opposite each other. Possibly it was adjacent to the left counter quadrant that the daughter met with the least resistance to corallite expansion.

During the early part of the hystero-neanic stage, major septa do not reach the axis, but they lengthen with further corallite development so that by the end of the hystero-neanic stage, some extend to the axis and an irregular axial structure is consistently present.

Throughout the hystero-neanic stage, the daughter corallite is subcircular in outline and lonsdaleoid dissepiments are absent, except for the occasional small one. Interseptal dissepiments are absent at first, but by the end of this stage of development, a single row is developed entirely around the corallite.

Approximately 2·75 mm. of growth occurs during the hystero-neanic stage. The end of this stage and the commencement of the late neanic stage are transitional.

Late neanic stage (F46028/39-72): The daughter corallite now acquires sharp corners and some lonsdaleoid dissepiments. A few pairs of major septa alternating with minor septa in order of appearance, are inserted at the wall in the cardinal and alar fossulae. A small axial structure of twisted lamellae is present until just before the achievement of the ephebic stage; in some corallites this axial structure persists into adulthood. Little development of the lonsdaleoid dissepimentarium occurs until the later part of this stage. At this time, a wide zone of lonsdaleoid dissepiments develops around the corallite, and many of these dissepiments become naotically modified. With this development, the corallite reaches adulthood, after 20 mm. of growth during this stage and a total of about 23 mm. of growth.

Parricidal peripheral increase.

In the observed example of parricidal peripheral increase, four corallites arose in the calice of the parent, and these soon expanded to occupy the entire area of the calice. A fifth corallite appeared somewhat later than the rest and may have arisen by lateral increase from its developing neighbour. The early stages of development of these corallites have been destroyed by crushing. In general, their hystero-ontogeny resembles that observed in the above described example of lateral increase, except that a lonsdaleoid dissepimentarium is developed earlier, but nevertheless not widened nor naotically modified until the final stage of development. Three of these corallites are illustrated in the lower-left of pl. XIII, fig. 1.

Remarks: The variable nature of the adult morphology of the species is likewise reflected in the nature of corallite development, and it is difficult to assess which features of the latter are typical of the species. Certainly the character of axial septa ceasing to oppose one another after early development in the example illustrated is one of individual variation, and so also is the exact pattern of septal insertion. However, the rather general pattern during hystero-neanic development of major septa appearing before the minor septa in the cardinal quadrants, and major and minor septa appearing alternately in the counter quadrants, is probably fairly typical of the species; it somewhat resembles insertion in laterally arising corallites of *Lithostrotion* (see Jull, 1965). Other apparently significant characters are the initially united axial septa which are radially orientated with respect to the axis of the parent during hystero-brephic development; and the late neanic appearance of an irregular axial structure and of lonsdaleoid dissepiments which are mainly formed as such and not as modifications from interseptal dissepiments.

Increase in *A. hallense* differs in a number of characters from that in the type species of *Thysanophyllum*, *T. orientale* Thomson and in *Lonsdaleia* spp. (see Jull, 1967). United axial septa during hystero-brephic development, and minor septa appearing in the counter quadrants at the start of the hystero-neanic stage are unknown in *T. orientale* and *Lonsdaleia.* They also generally lack the formation of lonsdaleoid dissepiments *per se*, these structures forming rather from interseptal dissepiments by the withdrawal of septa from the wall.

In lateral increase in *Lonsdaleia*, commonly as many as five corallites develop nearly simultaneously from the same parent and some of these corallites are orientated with their axial planes as much as 90 degrees away from the parent; neither of these characters have yet been observed in either *A. hallense* or *T. orientale.*

APHROPHYLLUM SMITHI, sp. nov.

(Pl. XIII, figs 4–5)

Holotype: F46073, from L2816, located in Viséan limestones at Halls Creek 300 yards north along strike from Bingara Falls, Portion 62, Parish Hall, County Murchison, New South Wales.

Diagnosis: Similar to *A. hallense* but with smaller corallites having fewer septa, a narrower lonsdaleoid dissepimentarium, and flatter tabulae.

Description: Based on the holotype and three topotypes, all of which have been partially crushed.

The corallum is cerioid and consists of irregularly shaped polygonal corallites which average 11 mm. and range from 7·5 to 14 mm. in diameter. Intercorallite walls are sinuous or undulating as seen in transverse section of the corallite, and are 0·4 to 0·5 mm. in width. Stereome lines the dissepiments and in some corallites, it may almost totally infill the interstices of the skeletal elements.

Septa are straight or slightly wavy and have irregular outlines. Corallites have from 18 to 22 septa of each order. Major septa generally do not reach the axis in the holotype, but in most corallites of the other specimens (pl. XIII, fig. 5) they extend close to the axis or reach it. Long septa are pinnately arranged in elongate corallites. An axial structure is absent. Minor septa are less than half as long as major septa.

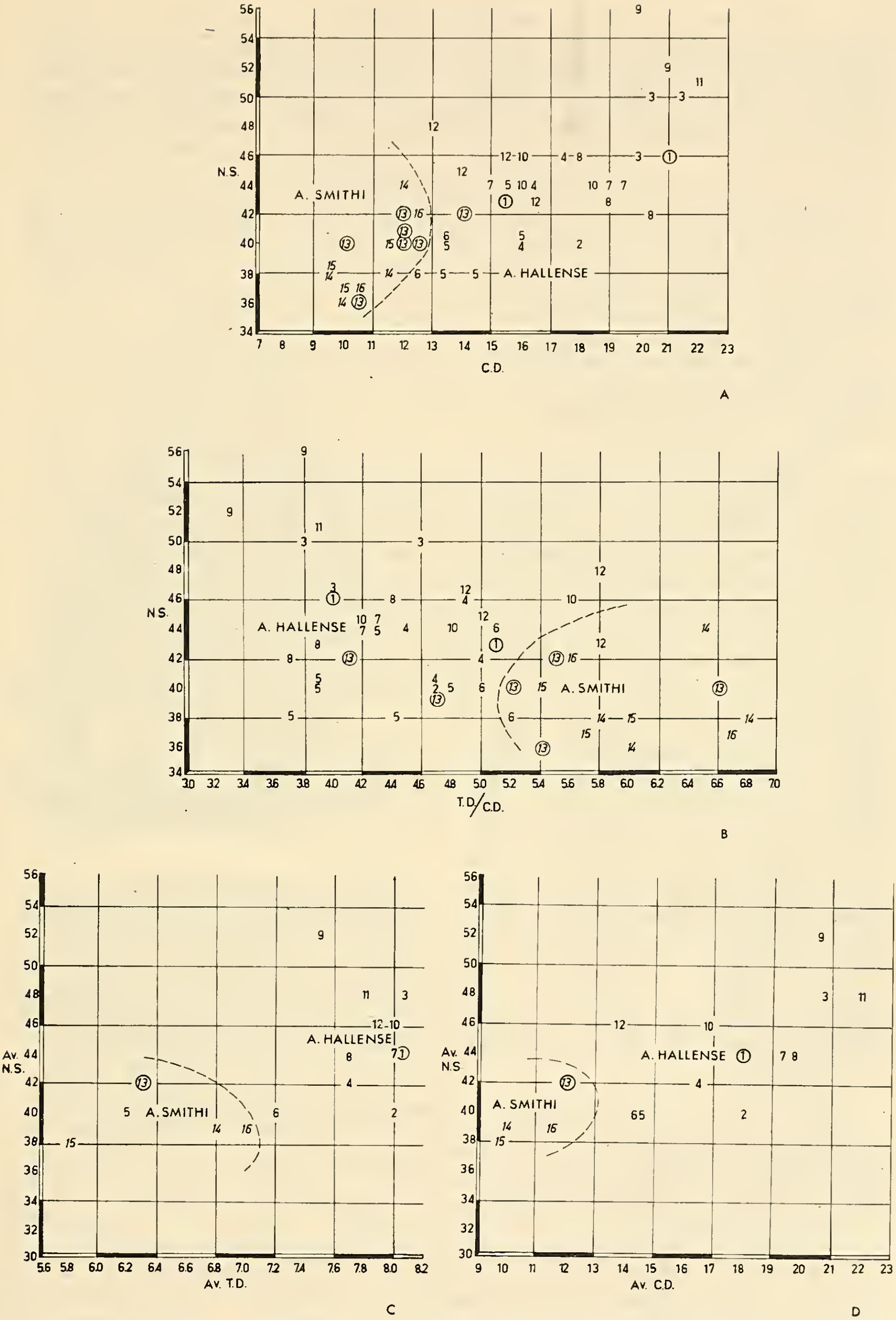
The dissepimentarium consists of one to three rows of steeply inclined interseptal dissepiments bounded by variably developed lonsdaleoid dissepiments which are usually crushed. Lonsdaleoid dissepiments are developed entirely around the corallite, or are present only in a narrow zone in the corners or ends of corallites. Naotic developments are uncommon. The tabularium ranges from 5·5 to 7 mm. in diameter. Tabulae are gently arched or domed if septa extend close to the axis, or flat or sagging if septa are short. The ends of tabulae are flat or upturned, and approximately 20 tabulae occur in a 10 mm. interval.

Hystero-ontogeny: The few youthful corallites observed appear to have arisen by lateral increase. They are similar to those in *A. hallense*, but an axial structure was not observed.

Microstructures: Septal trabeculae are monacanthine and similar to those in *A. hallense* (see Text-fig. 4) except that trabeculae are more closely spaced, being at approximately 0·075 mm. intervals, rather than 0·1 to 0·125 mm. as they are in *A. hallense.*

Distribution: The species is known only at the type locality.

Remarks: The species is named in honour of Dr. Stanley Smith who first described corals from the limestones at Halls Creek. Apart from possessing



Text-fig. 3. Graphical comparison of *Aphrophyllum smithi*, sp. nov. and *A. hallense* Smith. N.S. = number of septa of both orders; C.D. = corallite diameter (the mean of the maximum and minimum dimensions in mm.); T.D. = tabularium diameter (in mm.); Av. = average. Each corallum studied was assigned a number, and all corallites measured in a corallum are recorded on the graphs with the number of their particular corallum. Vertical numbers are of corallites in *A. hallense*, and inclined numbers are of *A. smithi*. Circled numbers are of corallites in the holotypes. Only uncrushed or slightly crushed corallites were measured.

smaller dimensions overall, *A. smithi* is similar to *A. hallense*, and larger than average corallites in this species may be mistaken for *A. hallense* although corallites of the latter usually have a wider lonsdaleoid dissepimentarium and more strongly arched tabulae. The two are graphically compared in Text-fig. 3, and some overlap in parameters is evident, especially in graph B.

Affinities of Aphrophyllum

Although the adult and youthful morphology of *A. hallense* is now well known, the affinities of the genus are still not readily evident. This is partly due to the paucity of information on the hystero-ontogeny of rugose corals in general so that the significance of particular characters is yet not fully appreciated.

Aphrophyllum was considered by both Hill (1956, p. F290) and Dobrolyubova (1962, p. 316) to be related to *Palaeosmilia*; Hill placed the genus in the Amygdalophyllinae.

For the following reasons, however, the affinities of the genus might appear to be with the Lonsdaleiidae, as was first suggested by Pickett (1967). The tabulae of *A. hallense* and *A. smithi* resemble those in *Thysanophyllum orientale*; this last species, the type of *Thysanophyllum*, was concluded by Jull (1967) to lie in the Lonsdaleiidae. When naotic developments are absent in *Aphrophyllum*, a common situation in this genus, the lonsdaleoid dissepimentarium is similar to that in typical lonsdaleid corals. Moreover, corallites of *Aphrophyllum* in which septa do not reach the axial region closely resemble the typical morphology of *Thysanophyllum*; this especially applies to some undescribed Queensland species, such as *Aphrophyllum* sp. illustrated by Hill and Woods (1964, pl. C2, fig. 1).

Other characters of *Aphrophyllum*, on the other hand, are unknown in typical representatives of *Lonsdaleia* and *Thysanophyllum*. These are the pinnate arrangement of septa in all known species of *Aphrophyllum*, some details of the hystero-ontogeny of *A. hallense*, as discussed above, and the nature of the axial structure.

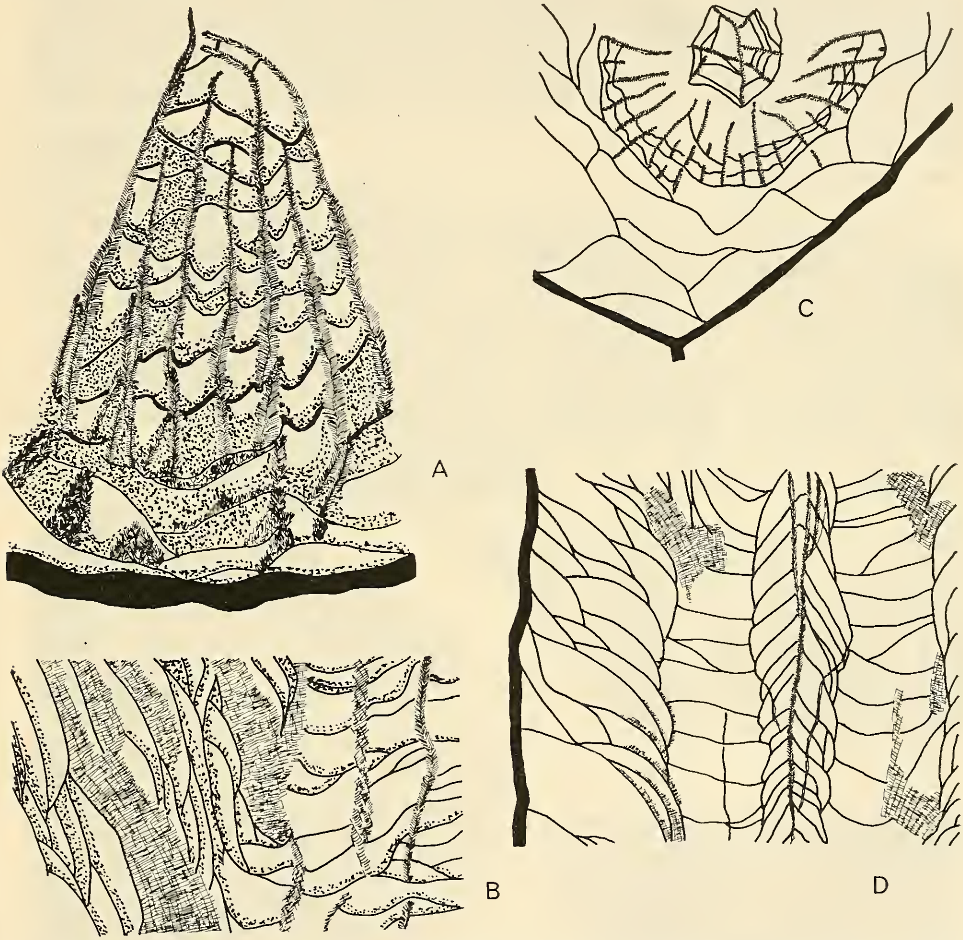
Septa in *Aphrophyllum*, *Lonsdaleia* and *Thysanophyllum* are composed of monacanthine trabeculae (Text-fig. 4). In *A. hallense*, trabeculae are larger than is normal in these other genera, and the peripheral ends of septa in some corallites are composed of two or more rows of trabeculae and may be split or cavernous. Multiple rows of trabeculae are a common situation in some corals showing naotic developments, but are unknown in *Lonsdaleia* and *Thysanophyllum*. Wang (1950) has earlier remarked on septal structure in these genera.

There is thus a strong suggestion that *Aphrophyllum* lies in a separate, new family of rugose corals. Further work on other species of *Aphrophyllum* is currently in progress by the writer and may assist in elucidating the taxonomic position of this genus.

Finally, Smith (1920, p. 55) and Jones (1933, p. 60) have both remarked on the similarity of *Aphrophyllum hallense* to *Endophyllum*; superficially at least, the former differs significantly only by having naotically modified dissepiments. *Endophyllum* is widely distributed in Middle to Upper Devonian beds and three cerioid species described by Gorsky (1935) from the Tournaisian of Novaya Zemlya appear to belong to the genus (see Soshkina and Dobrolyubova, 1962). Possibly hystero-ontogenetic studies of *Endophyllum* may show that *Aphrophyllum* is descended from this line.

Acknowledgements

I am very grateful to Professor D. Hill, F.R.S., both for her criticism of the manuscript of this paper and her advice during my studies at the University of Queensland, of which this paper is part of the outcome. Mr. O. H. Fletcher, formerly of the Australian Museum, Sydney, helpfully provided photographs and information on the type material of *A. hallense*, and I gladly acknowledge the assistance of Dr. B. Runnegar, of the University of New England, during our visit to the Halls Creek area in 1964 to collect the present material.



Text-fig. 4. Monacanthine septal trabeculae in A, B, *Aphrophyllum hallense* Smith, F46043 from L2816, and in C, D, *Lonsdaleia floriformis floriformis* (Martin), B.M. R17160, from Viséan D_2 zone beds at Coalbrookdale, Shropshire, England. All figs approx. ×7.

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EXPLANATION OF PLATE XIII

All figures × 2.

Figs 1–3. *Aphrophyllum hallense* Smith. 1, transverse section of F46028 from L2816; 2, transverse section of topotype, AM 1037; 3a–b, transverse and longitudinal sections of F46071 from L2817.

Figs 4–5. *Aphrophyllum smithi*, sp. nov. 4a–b, transverse and longitudinal sections of holotype, F46073 from L2816; 5, transverse section of topotype F46074 from L2816.